# Repeatability in spring arrival dates in Pied Flycatchers varies among years and sexes

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Timing of arrival in long-distance migration could have fitness consequences: arrival too early impairs survival chances, whereas arrival too late reduces current reproductive success. Evolution thus may have favoured a phenotype that arrived at the optimal time. However, individuals within populations of long-distance migrant species arrive over a considerable time span, and often show consistency in whether they are early or late. This repeatability in arrival varies between studies, and we hypothesise it to be affected by conditions encountered en route or in winter. Here we report on the spring arrival dates of Pied Flycatchers *Ficedula hypoleuca* to their Dutch breeding sites during eight consecutive years. Our field estimates of arrival were highly accurate, as validated by geolocator data on 13 individuals. Years differed in mean arrival dates. Within years and sexes, arrival date generally spanned more than two weeks. First-year individuals arrived on average 4–5 days later than older individuals. Using repeated arrival dates of more than 500 individuals we show that (1) the overall arrival repeatabilities were similar for females and males, (2) arrival repeatabilities varied temporally, with individuals in consecutive years having sometimes moderate ($R$ = 0.2) and sometimes rather high (>0.40) repeatabilities, and (3) individual females arrived later in their first than in their second year. In females, repeatabilities of arrival and laying dates were similar. We hypothesize that individual flycatchers have a high individual consistency in their spring migration departure date from the wintering grounds. However, previous studies suggest the expression of this individual schedule to be affected by environmental circumstances at the wintering grounds or by what is encountered en route, determining whether this variation is still present at arrival on the breeding grounds. Sexes seemed to differ in this respect, as year-to-year variation in repeatabilities of timing was explained by individual consistency in females, but not in males. We discuss the relevance of the observed variation for the potential for an evolutionary response when environments change.

Key words: *Ficedula hypoleuca*, migration, timing, repeatability

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Migration is all about being at the right place at the right time. In this way, migrants make use of seasonal variation in habitat suitability, and timing of movements has evolved to match needs with requirements (Alerstam 1990). However, seasonal patterns in habitat suitability fluctuate between years, with sometimes severe fitness consequences if birds arrive too early or too late (Brown & Brown 2000, Smith & Moore 2005, Newton 2007). In particular, spring migration towards the breeding grounds seems to be most sensitive to between-year variation in ecological conditions (Studds & Marra 2011, Klaassen *et al.* 2014, Lok *et al.* 2015). At this time of year, individuals migrate against a gradient of habitat suitability (at least for insectivores), with

conditions becoming more hostile with proximity to the breeding grounds, and only improving after birds have arrived there.

Migration is a sequence of decisions on when to depart in what condition, how long to fly, and where and when to stop-over, and again when to depart for the next migratory leg (Alerstam 1990). The longer the migratory journey, the less likely that circumstances at departure predict circumstances at the breeding site (Hötker 2002). However, the closer that individuals get to their destination, the more they can anticipate the specific conditions in that year (Marra *et al.* 2005). Individual flexibility to between-year variation in breeding site phenology thus likely arises through incorporating variation during the latter part of the migratory journey (but see Fraser *et al.* 2013 for lack of adjustment to a warm spring). At the population level, correlations between arrival date and circumstances en route have indeed been found (Ahola *et al.* 2004, Both *et al.* 2005, Marra *et al.* 2005, Jonzén *et al.* 2006), and in a few cases this was shown to be caused by phenotypic plasticity (Saino *et al.* 2007, Balbontín *et al.* 2009).

If circumstances are unpredictable, little phenotypic plasticity is expected (Botero *et al.* 2015), and under such conditions consistent individual variation may have been favoured over time. Across breeding population studies of long-distance migrants, the mean repeatability of spring arrival is 0.31 (range 0.05–0.63, Table 1), a value that is common for many other behavioural traits (Bell *et al.* 2009). Individual consistency might be expected if arrival conditions are unpredictable at departure from distant wintering grounds (Coppack & Both 2002), but environmental conditions encountered during the journey may strongly affect whether individual consistency could still be expressed after a long journey. The observed variation in arrival repeatability among studies could result from species- and population-specific differences in whether such consistent individual variation exists in annual schedules, but also from environmental variation that differs among the years of study. Especially for arrival dates, a whole array of behavioural decisions regarding departure, flights and stop-overs is influenced by the environmental conditions encountered (see e.g. Senner *et al.* 2015), and therefore initial individual variation in migration schedules could have vanished by the time birds arrive at their breeding grounds, but could also have been exacerbated (Winkler *et al.* 2015).

In a world that is changing rapidly, it is important to understand how species adapt and what constrains adaptation. With ongoing climate change, long-distance migrants have sometimes advanced their migration timing (Jonzén *et al.* 2006, Lehikoinen & Sparks 2010), but in many cases have not, or did so too slowly to anticipate the phenological advances of their breeding grounds (Both & Visser 2001). The presumed low predictability of breeding ground conditions at departure suggests that observed advances in arrival are either due to phenotypic plasticity at the end part of the migratory journey, or the result of a systematic change in departure date due to ontogeny or evolution (Coppack & Both 2002, Ahola *et al.* 2004, Both 2010, Gill *et al.* 2014). So far, little empirical evidence exists on whether variation in arrival date has a genetic background (Potti 1998, Møller 2001, Charmantier & Gienapp 2014, Tarka *et al.* 2015), and whether the observed advances in arrival date are the result of selection on a genetically determined trait (Gienapp *et al.* 2007, Merila 2012).

Our study focuses on spring arrival dates in a long-distance migrant passerine, the Pied Flycatcher *Ficedula hypoleuca*. Timing of migration in this species is partly governed by photoperiods: in lab conditions, flycatchers only started spring migration when given photoperiodic cues of the normal wintering area (Gwinner 1996). Recent data from geolocators showed that males from our Dutch breeding population winter in eastern Guinea and western Ivory Coast (c. 5–9°W), depart from the wintering grounds around the beginning of April and cover the 5000 km in about 18 days (Ouwehand *et al.* 2015). Ring recoveries in northern Africa suggest that migration dates have advanced for our population, but we have yet no proof for an advance in spring arrival date (Hüppop & Winkel 2006, Both 2010). We have argued that conditions en route and lack of predictability of conditions during migration may prevent birds arriving earlier, despite the advance in spring phenology of the breeding ecosystem (Both 2010, Winkler *et al.* 2015). Arrival and breeding dates have indeed been shown to correlate with environmental conditions en route (Ahola *et al.* 2004, Both *et al.* 2006, Hüppop & Winkel 2006). If this environmental effect is strong and fluctuates strongly between years, potential individual variation in departure date from the wintering grounds may not be visible upon arrival at the breeding grounds. The only study that addressed repeatability in arrival dates in Pied Flycatchers was performed in Spain, which found no repeatability for males (Potti 1998), whereas females had repeatable arrival dates ($R = 0.29$; Potti 1999).

The aim of this paper is to describe repeatability in spring arrival date in Pied Flycatchers. Understanding the variation in repeatability in arrival dates is a first

**Table 1.** Review of published data on repeatability of spring migration timing and arrival in long-distance migratory birds. Sex: FM males and females included, Stan: data standardized to annual mean (Y) or not (N). Focus: winter: only winter population sampled, breed-winter: both winter and breeding populations sampled, breed: only breeding population sampled.

| Species | Sex | Stan | Focus | Repeatability (SE) | | *n* ind | # year | Obs/ Ind | Source |
|---|---|---|---|---|---|---|---|---|---|
| **Spring Departure** | | | | | | | | | |
| Bewick's Swan | FM | Y | Winter | 0.06 | (0.03) | 67 | 20 | 12.37 | Rees 1989 |
| Egyptian Vulture | FM | | Breed | 0.43 | | 6 | 7 | 3.83 | López-López *et al.* 2014 |
| Black Kite (2–6 yrs old) | FM | N | Breed | 0.46 | (0.13) | 22 | | | Sergio *et al.* 2014 |
| Black Kite (7–11 yrs old) | FM | N | Breed | 0.80 | (0.14) | 10 | | | Sergio *et al.* 2014 |
| Bar-tailed Godwit, Older | FM | N | Winter | 0.82 | (0.03) | 49 | 3 | 2.20 | Conklin *et al.* 2010 |
| Bar-tailed Godwit, Imm. | FM | N | Winter | 0.38 | | 12 | 3 | 2.00 | Battley 2006 |
| Wood Thrush | FM | N | Breed-Winter | 0.71 | | 10 | 3 | 2.00 | Stanley *et al.* 2012 |
| American Redstart | FM | Y | Winter | 0.38 | | 74 | 5 | 2.64 | Studds & Marra 2011 |
| **Spring passage/stop-over departure** | | | | | | | | | |
| Greater Snow Goose | F | N | Breed | –0.02 | | 20 | 3 | 2.05 | Bety *et al.* 2004 |
| Black-tailed Godwit | M | N | Breed | 0.30 | (0.07) | 20 | 4 | 2.85 | Lourenço *et al.* 2011 |
| Black-tailed Godwit | F | N | Breed | 0.42 | (0.09) | 31 | 4 | 2.70 | Lourenço *et al.* 2011 |
| Bar-tailed Godwit | FM | N | Winter | 0.92 | (0.04) | 8 | 2 | 2.00 | Conklin *et al.* 2013 |
| Wood Thrush | FM | N | Breed-Winter | 0.49 | | 10 | 3 | 2.00 | Stanley *et al.* 2012 |
| **Spring arrival** | | | | | | | | | |
| Scopoli's Shearwater | M | | Breed | 0.20 | | 7 | 3 | 2.14 | Muller *et al.* 2014 |
| Scopoli's Shearwater | F | | Breed | 0.00 | | 5 | 3 | 2.20 | Muller *et al.* 2014 |
| Cory's Shearwater | FM | | Breed | >0.51 | | 14 | 3 | 2.07 | Dias *et al.* 2011 |
| Emperor Goose | F | Y | Breed | 0.34 | (0.16) | 18 | 4 | 2.78 | Petersen 1992 |
| Greater Snow Goose | F | N | Breed | 0.42 | | 20 | 3 | 2.05 | Bety *et al.* 2004 |
| Egyptian Vulture | FM | | Breed | 0.56 | | 6 | 7 | 3.83 | López-López *et al.* 2014 |
| Black Kite (2–6 yrs old) | FM | N | Breed | 0.44 | (0.23) | 22 | | | Sergio *et al.* 2014 |
| Black Kite (7–11 yrs old) | FM | N | Breed | 0.67 | (0.20) | 10 | | | Sergio *et al.* 2014 |
| Marsh Harrier | FM | N | Breed | 0.63 | | 3 | | 5.00 | Vardanis *et al.* In Thorup *et al.* 2013 |
| Osprey | FM | N | Breed | 0.07 | | 4 | | 3.25 | Vardanis *et al.* In Thorup *et al.* 2013 |
| Black-tailed Godwit | FM | N | Breed | 0.51 | | 54 | 14 | 5.30 | Gill *et al.* 2014 |
| Black-tailed Godwit | FM | N | Breed | 0.18 | | 46 | 6 | 3.33 | Gunnarsson *et al.* 2006 |
| Black-tailed Godwit | M | N | Breed | 0.18 | (0.02) | 70 | 6 | 3.27 | Lourenço *et al.* 2011 |
| Black-tailed Godwit | F | N | Breed | 0.29 | (0.03) | 81 | 6 | 2.91 | Lourenço *et al.* 2011 |
| Bar-tailed Godwit | FM | N | Winter | 0.91 | (0.05) | 8 | 2 | 2.00 | Conklin *et al.* 2013 |
| Common Tern, all | FM | Y | Breed | 0.20 | (0.02) | 1232 | 15 | 4.31 | Arnaud *et al.* 2013 |
| Common Tern, experienced | FM | Y | Breed | 0.35 | (0.02) | 648 | 15 | 4.35 | Arnaud *et al.* 2013 |
| Barn Swallow | M | N | Breed | 0.51 | | 23 | 16 | 2.38 | Møller 2001 |
| Barn Swallow | M | N | Breed | 0.50 | | 15 | 2 | 2.00 | Ninni *et al.* 2004 |
| Cliff Swallow | FM | Y | Breed | 0.09 | | 14,031 | 16 | | Brown & Brown 1998 |
| Great Reed Warbler | FM | Y | Breed | 0.37 | (0.04) | 548 | 20 | 1.89 | Tarka *et al.* 2015 |
| Dusky Warbler | M | Y | Breed | 0.34 | | 12 | 3 | 2.00 | Forstmeier 2002 |
| Eastern Kingbird | M | Y | Breed | 0.05 | | 30 | 4 | 2.47 | Cooper *et al.* 2009 |
| Eastern Kingbird, older | F | Y | Breed | 0.39 | | 19 | 4 | 2.31 | Cooper *et al.* 2009 |
| Eastern Kingbird | F | Y | Breed | 0.21 | | 26 | 4 | 2.31 | Cooper *et al.* 2009 |
| Wood Thrush | FM | N | Breed-Winter | 0.66 | | 9 | 3 | 2.00 | Stanley *et al.* 2012 |
| Pied Flycatcher | M | Y | Breed | 0.08 | | 39 | 4 | 2.26 | Potti 1998 |
| Pied Flycatcher | F | Y | Breed | 0.29 | 0.17 | 77 | 5 | 2.21 | Potti 1999 |
| Pied Flycatcher | M | Y | Breed | 0.27 | 0.03 | 307 | 7 | 2.31 | This study |
| Pied Flycatcher | F | Y | Breed | 0.30 | 0.04 | 221 | 7 | 2.39 | This study |

step for the analysis of a genetic basis for this trait. Because repeatability is likely to be influenced by the extent of variation in arrival dates in the population, we first describe for our eight consecutive years of observations the variation in arrival dates of males and females separately. Next we test whether age affects arrival date. Finally, we analyse repeatability in spring arrival dates for individual males and females separately and compare these with repeatability in laying dates. We expect that repeatability in arrival date is individual-, age- and sex-specific, with variations in conjunction with year-specific environmental conditions during winter and/or migration. In this paper we do not aim to identify these year-specific environmental conditions.

## METHODS

Pied Flycatchers are small (12–13 g) insectivorous long-distance migrants that winter in West-Africa and breed in Europe and Western Siberia. They readily accept nest boxes for breeding, and our observations were performed in 8 study plots with 100 nest boxes each, and two with 50 and 65 nest boxes in Drenthe, The Netherlands (52°49'N, 6°22'E). The nest boxes were placed in February–March 2007 before arrival of the flycatchers. The arrival data of 2007 are likely biased because most birds breeding on the plots that year first had to discover the plots. Study plots of 100 boxes were on average 50 ha in size, and were situated in two larger forested areas (Dwingelderveld and Drents-Friese Wold). Habitats ranged from pure deciduous stands (mostly *Quercus robus*) to mostly coniferous (mostly *Pinus sylvestrus*) and different mixtures of both coniferous and deciduous species. The distance between adjacent plots varied between 2.5 and 15 km. The total breeding population increased from c. 150 pairs in 2007 to c. 280 in 2010 and remained rather stable afterwards (until 2014).

### Observations

Spring arrival dates were determined through field observations in 10 study plots, which were visited on average once every other day. One of us (RGB) checked one plot and its surroundings every day from mid-March onwards. If the first flycatcher was observed here before 5 April, or when Pied Flycatchers were recorded that early on the citizen science web site (www.waarneming.nl), we also started our observations on other plots. Otherwise, six trained observers started recording arrivals from 5 April until around 10 May (and less systematically later on). We did observe some occasional late-arriving flycatchers that started singing within our study plots (up to 25 May), and it is possible that a few more individuals arrived this late but remained unnoticed. Late arrivals could be individuals, especially females, that had attempted to breed somewhere else, but whose nests had been disturbed.

During an observation session, the plot was crossed on foot and all signs of Pied Flycatcher presence were noted. Observations started just after sunrise until around noon. Per plot a session lasted between 1 and 3 h, depending on the number of flycatchers present (10–60 breeding pairs per plot).

Upon arrival, individual males were identified by means of plumage traits and presence/absence of (colour)rings. In our population, males greatly vary in plumage characteristics (i.e. number, size and shape of forehead patches, darkness of dorsal feathers, size of white wing patches). These data were validated with information we gathered when males were captured during the chick-rearing stage. Pied Flycatcher males commonly breed in the immediate surroundings of the area where they are first observed singing (see Potti & Montalvo 1991a, Visser *et al.* 2015 for similar approach). Arrival date equals first observation day when the plot was visited daily, otherwise the midpoint was used between the observation day and the previous visit. Out of 1962 potential plot-observation days between first arrival and 2 May, there were 24 cases with three days in between subsequent visits to a plot, and in nine cases four days. Given the high detection probability of individual males (see next paragraph) and the high visit frequency to the plots, we feel confident that our arrival scores accurately estimate real arrival date on the study plots.

Females behave more cryptically than males, and we record their arrival as the date they became paired. Previous studies support the notion that females pair up within a few hours after arrival (Dale *et al.* 1992). Pairing date was easily measured, because male behaviour changed drastically upon a female's arrival: soft warbling notes replaced the persistent and full song, or males became silent. When males failed to advertise their presence in occupied territories, we took extra effort to find the male and his mate and checked the nearest boxes for nesting material. Pairing date or date of first nesting material in the nest box (often on the same date) were equated with female arrival date. In cases when we had not been in the area on the previous one or two days, we adjusted the estimated female arrival from the state of nest-building: no or little material was interpreted as arrival on the observation day,

Male Pied Flycatcher proclaiming its territory at the morning of arrival to its territory (photo: Richard Ubels, 19 April 2013).

nesting material without a nest cup as the day before and nests with partial or full nest cup as two days earlier. Some arrival dates of females were disregarded, i.e. when the female apparently disappeared within a few days of pairing and initial nest-building (e.g. four out of 113 female arrivals in 2010, two out of 89 in 2012, and two out of 66 in 2014). These cases were evident from males starting to sing again. We captured most females during incubation, when we matched arrival with female identity based on their ring numbers. In some years we used aluminium colour rings for individual identification, but stopped this practise again because these rings got damaged after some years with possible leg injuries as a result.

**Accuracy of arrival date**

When we measured spring arrival we assumed that birds did not first try to settle somewhere outside our study plots (but see below for exceptions). This assumption was validated with an independently estimated arrival date for 12 male and one female flycatcher equipped with a geolocator in 2012 ($n$ = 2), 2013 ($n$ = 2) and 2014 ($n$ = 9). Arrival dates from light-level geolocators correlated well with arrival dates assessed in the field: $r$ = 0.98, $n$ = 13, $P$ < 0.001. This estimate was not affected by including multiple years and sexes, because when considering the biggest group (males in 2014, $n$ = 8) the correlation was still $r$ = 0.98. On average, the arrival date derived on the basis of visual observations was 1.57 d (range –1 to +5) later than what was estimated on the basis of the geolocation data. The only female in this sample had exactly the same arrival date as scored via field observations.

The accuracy of arrival date depends on the detectability of a bird. For four years we calculated for part of the dataset the daily detection probability of males recorded during each visit between the first day he was observed until he was paired. In 2008 this probability was 84% (measured for 72 males, with 195 potential individual observation days), for 2010 it was 82% ($n$ = 113/437), for 2012 it was 85% ($n$ = 69/212) and in 2014 95% ($n$ = 62/517). Males failing to attract a female had a similar probability of being observed (estimated for 30 males in 2014 from arrival until 6 May: 92%). If females do not immediately start nest building, their arrival dates depend on our ability to observe males with or without their females. The possibility exists that female arrival is biased towards later

dates, because males were less often detected after females arrived. This was not the case, as detection rates of males the day before we assigned the pairing dates were not lower than before, suggesting that we accurately observed pairing date (observation probability day before paired: 2008: 80% ($n$ = 37), 2010: 76% ($n$ = 76), 2012: 93% ($n$ = 27) , 2014: 98% ($n$ = 46)).

Some males may move to another site after first settlement, as proven by two individuals. A colour-ringed male was recorded on 20 and 22 April 2012, but not seen here from 23 April onwards. He re-emerged singing at a nest box 2.4 km away on 25 April, in another study plot. This individual had been breeding in 2011 in the same box where he was observed on 20–22 April 2012, but this box happened to be occupied by Great Tits *Parus major*; all other boxes within 200 m of this box were also occupied. Interestingly, this individual (born in 2008) eventually settled just 270 m from his natal box, paired up with a female a week later and bred successfully at this new spot. The other individual arrived on 16 April 2013 near the nest box where he had bred the previous year. This individual was seen singing on all visits until 6 May (and was caught on 27 April). Around 9 May his nest box was usurped by Great Tits, and he moved to another plot, c. 2.4 km away, where he was caught on 27 May. As with the previous male, this male moved towards his natal area, where he was caught 130 m away from where he was born. This male was not observed singing for a long period, and did not breed after moving. Such movements may have occurred more frequently and some of the later-arriving individuals could have arrived earlier elsewhere before moving again. Inclusion of these individuals will increase the phenotypic variance, and thereby most likely biases repeatability estimates downwards.

**Data selection**

We only included arrival dates of individuals that were caught later in the year, and for which individual identity was unequivocally determined. We excluded birds when: (1) the hatching date of their brood was experimentally advanced or delayed by more than one day the year before they arrived (both for adults and offspring), (2) they were carrying a geolocator, (3) they were translocated to another breeding site one or more years before the arrival year, or (4) when their arrival dates were later than 19 May.

We recorded 1581 arrival dates of individually identified males. In 459 cases we scored male arrival without obtaining their identity, but these were excluded from further analyses. About half of the latter cases involved a male that had been singing for two or more days, but disappeared after a couple of days. In 208 cases males obtained a female that laid eggs, but nests failed before the male was caught (mostly due to predation), or we failed to capture the male. In females with known identity, we recorded 1650 arrival dates. In most cases these females laid eggs, but some were depredated before we caught them.

Age is defined as first year when born one year ago, second year is born two years ago, etc. Age effects are only tested for individuals ringed as nestlings, because ageing in full-grown birds is not always reliable. Note that many locally born individuals are not observed in their first year (Harvey *et al.* 1985, Sternberg 1989, Potti & Montalvo 1991b). While analysing the age effect we also have to consider whether previous experience affects arrival date (Sternberg 1989, Sternberg *et al.* 2002, Sergio *et al.* 2014).

In the repeatability analysis we included 221 females and 307 males for which we had multiple observations during their life. Apart from the selection criteria above, we excluded the data for 2007 because our study plots were newly created and most individuals still had to discover the nest box area; this may have affected their arrival date at their eventual breeding spot. Furthermore, we excluded all first-year records of locally born individuals, as many individual flycatchers refrain from breeding in their first year and their arrival date may be affected by experience. For females, the number of individuals with 2, 3, 4, 5 and 6 years of observation were 158, 46, 12, 4 and 1 (average 2.39 observations per individual). For males these numbers were: 231, 58, 14, 4 and 0 (average 2.31 observations per individual).

**Analyses**

Arrival date distributions were in almost all years significantly different from normal (see results). As a result, most of the tests we provide are non-parametric (Kruskall–Wallis tests). When analysing age effects within individuals, we used paired $t$-tests.

Repeatabilities of arrival and laying dates were always analysed within a sex, and we used a mixed effects model implemented in the package rtpR (Nakagawa & Schielzeth 2010) in R statistical software (R Core Team 2012). We made use of REML estimation of repeatability, based on the individuals for which we had multiple observations. We analysed repeatabilities for absolute arrival dates and for arrival dates relative to the annual mean for the sex. Repeatability of laying date is given as a comparison, because laying date

repeatabilities are more often analysed, and we know that the estimate of first egg-laying date is with minor measurement error (given that we check our boxes at least once every five days and laying gaps are infrequent). We tested differences in repeatability estimates for different groups by bootstrapping 1000 estimates of both samples, and comparing for differences among these samples. The approximate *P*-value is twice the proportion of cases that are >= 0.

We tested temporal variation in repeatability by analysing the repeatability for all pairs of consecutive years and the individuals that bred in both years. These estimates were again from rtpR using the REML estimation and were only performed on relative arrival dates. We did not test formally whether samples for the same pairs of years differed among sexes using a bootstrap procedure, but tested whether the estimates (without standard error) for each pair of years differed systematically between the sexes using a paired *t*-test.

Repeatability describes how consistently individuals differ from each other (Conklin *et al.* 2013), which depends on how consistent individuals are, and how large differences are between individuals (total phenotypic variation). Low repeatabilities could thus be a result of low consistency within individuals, or alternatively through low variation among individuals. We calculated within-individual consistency between years as the absolute difference in arrival date: lower values mean higher consistency.

## RESULTS

### Variation between years

Arrival dates varied strongly, both within and between years (Figure 1). The earliest recorded male arrived on 26 March 2010, but in most years arrival started in the first or second week of April. The earliest female arrived on 8 April 2010; in most years female arrival started in the second week of April. Years differed in arrival dates for both sexes: the mean of the annual medians was for females 24.8 April (Table 2; range: 21–28; KW-test for differences between years: KW = 198.69, $n = 1650$, $P < 0.001$), and for males 17.9 April

**Table 2.** Summary data of annual variation in spring arrival dates of a population Pied Flycatchers in SW-Drenthe, The Netherlands, between 2007–2014. All dates are expressed in days from the first of April (31 = 1 May). *n* = number of individuals per year, Mean is the arithmetic mean arrival, SD the standard deviation, First is the first arrival date, Per10 the date at which the first 10% of the population arrived, Per90 the first 90%, and Last is the last observed arrival. 10–90% range is the number of days between Per10 and Per90. For each year we tested whether the observed distribution deviated from normality using a Shapiro–Wilk test, and test statistic and *P*-value are given.

| Year | *n* | Mean | SD | First | Per10 | Median | Per90 | Last | 10–90% range | SW-Stat | *P* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Females** | | | | | | | | | | | |
| 2007 | 102 | 26.49 | 6.95 | 16 | 18 | 24 | 35 | 48 | 17 | 0.906 | 0.001 |
| 2008 | 194 | 28.06 | 5.27 | 14 | 21 | 27 | 34 | 46.5 | 13 | 0.987 | 0.071 |
| 2009 | 199 | 28.37 | 6.83 | 12 | 18 | 28 | 37 | 49 | 19 | 0.989 | 0.127 |
| 2010 | 225 | 25.60 | 5.62 | 7.5 | 19 | 25 | 31 | 44 | 12 | 0.943 | 0.001 |
| 2011 | 237 | 22.65 | 6.89 | 9 | 13 | 22 | 33 | 43.5 | 20 | 0.975 | 0.001 |
| 2012 | 223 | 27.68 | 5.87 | 13.5 | 19 | 28 | 33 | 49 | 14 | 0.961 | 0.001 |
| 2013 | 251 | 22.95 | 6.23 | 13.5 | 15 | 21 | 30 | 44 | 15 | 0.919 | 0.001 |
| 2014 | 219 | 27.67 | 8.39 | 10.5 | 18 | 24 | 40 | 49 | 22 | 0.919 | 0.001 |
| Total | 1650 | 26.18 | 6.51 | 12.00 | 17.63 | 24.86 | 34.13 | 46.63 | 16.50 | | |
| **Males** | | | | | | | | | | | |
| 2007 | 87 | 20.85 | 5.53 | 9 | 12 | 21 | 26 | 33 | 14 | 0.965 | 0.018 |
| 2008 | 168 | 23.05 | 4.66 | 12 | 18 | 22 | 28 | 42 | 10 | 0.950 | 0.001 |
| 2009 | 183 | 18.87 | 8.50 | 3 | 7 | 17 | 28 | 49 | 21 | 0.964 | 0.001 |
| 2010 | 194 | 19.06 | 6.94 | –5 | 10 | 19 | 26 | 36.5 | 16 | 0.981 | 0.008 |
| 2011 | 213 | 13.95 | 5.89 | 3 | 6 | 12 | 22 | 32.5 | 16 | 0.958 | 0.001 |
| 2012 | 225 | 21.04 | 6.75 | 9 | 11 | 20 | 26 | 45 | 15 | 0.975 | 0.001 |
| 2013 | 254 | 17.95 | 4.69 | 13.5 | 14 | 16 | 22 | 49 | 8 | 0.703 | 0.001 |
| 2014 | 257 | 17.39 | 7.42 | 4 | 8 | 16 | 25 | 43 | 17 | 0.972 | 0.001 |
| Total | 1581 | 19.02 | 6.30 | 6.06 | 10.75 | 17.88 | 25.38 | 41.25 | 14.63 | | |

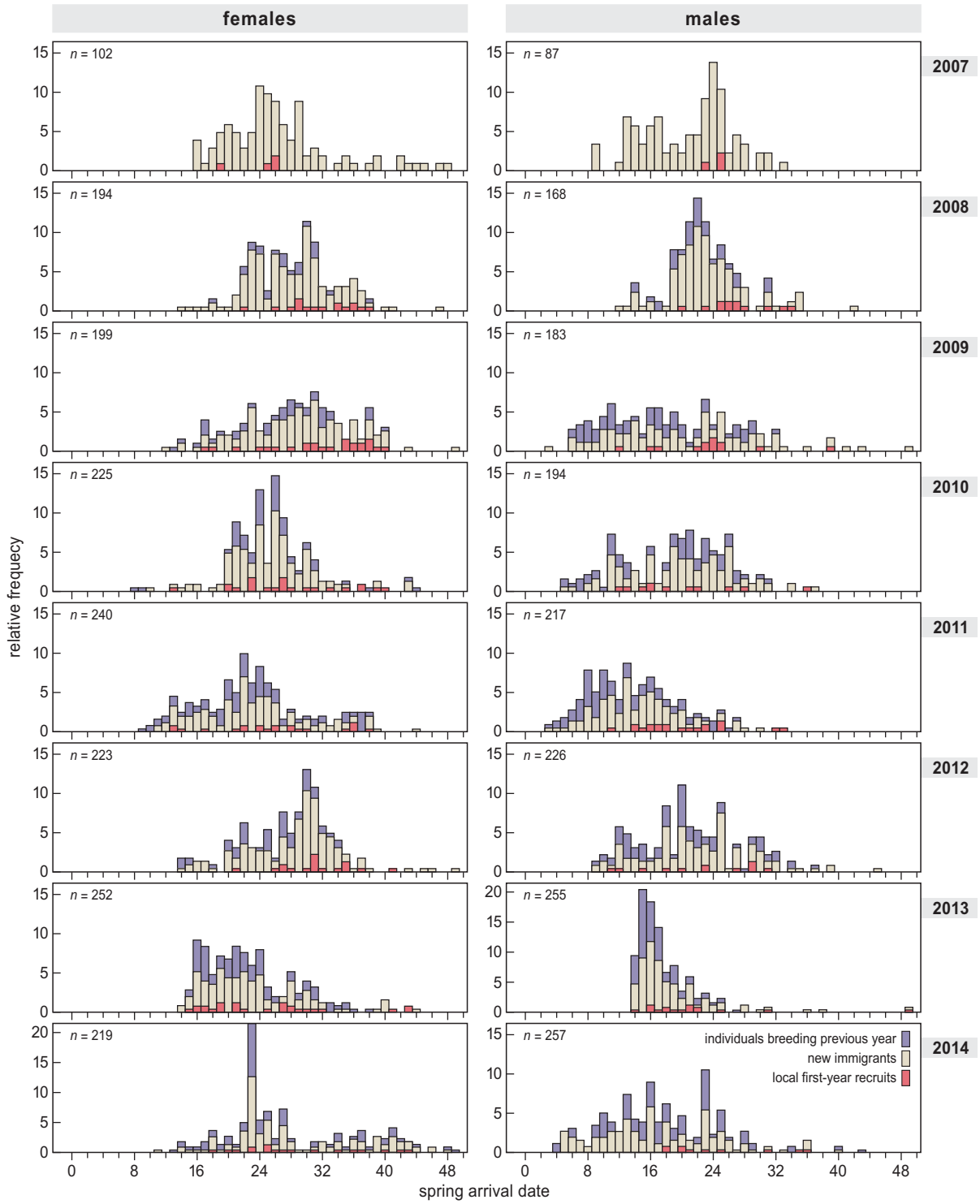


**Figure 1.** Frequency distribution of spring arrival date of individual Pied Flycatchers in Drenthe, The Netherlands, for all years in 2007–14. Shown are: local first-year recruits, individuals without previous experience in the area (new immigrants) and individuals breeding the previous year. Left panels: females, right panels: males. Note that for males in 2013 and females in 2014 the y-axis is different, due to a large fraction of individuals arriving on particular days. Numbers per year are given in the figure. Only individuals with known identity are included, excluding individuals that carried a geolocator, or had been experimentally delayed in the previous year.

(range 12–22; KW = 254.01, $n$ = 1581, $P < 0.001$). For each year and sex combination the frequency distribution deviated significantly from a normal distribution, except for females in 2008 and 2009 (see Table 2 for statistics). The average interval between 10 and 90% of the arrival distribution was for females 16.5 days (range 13–20), and for males 14.6 days (range 8–21). In males this interval was larger when the start of arrival (measured as the 10% percentile) was early (Pearson's correlation: $r$ = –0.83, $n$ = 8, $P$ = 0.01), whereas in females there was no clear support for such a correlation ($r$ = –0.48, $n$ = 8, $P$ = 0.22). Males showed more between-year variation in the start of arrival, whereas in females variation was larger at the end of the arrival distribution. The latter could have been the result of higher nest predation rates in some years, and late arriving females that had immigrated after losing their nest. Within 2008–14 there was a tendency of a positive correlation in median arrival dates of males and females ($r$ = 0.71, $P$ = 0.08), but not in their 10%- or 90%-percentiles ($r$ = 0.51, $P$ = 0.25; $r$ = 0.39, $P$ = 0.39).

Years with a warm start of April (e.g. 2009, 2011, 2014) also had an early start of male arrival, relative to years when this period was cold (supplementary material Figure 1; correlation between 10%-percentile of male arrival date and mean temperature 1–11 April: Pearson $r$ = –0.83, $n$ = 7, $P$ = 0.02; Inclusion of 2007 did not alter the result ($r$ = –0.81, $n$ = 8)). Start of female arrival was not clearly related to temperatures in early April (correlation between 10%-percentile of female arrival date and mean temperature 5–15 April: Pearson $r$ = –0.29, $n$ = 7, $P$ = 0.52).

**Age effects**

Females and males with known age arrived later in the first than in the second year (Figure 2A, B). In females this effect was only evident between the first and second year, with the medians being 28 and 24 April respectively (KW-statistic = 15.35, $n$ = 288, $P < 0.001$). In males this first-year effect was of similar magnitude as in females (first-year median 22 April, second year: 17 April; KW-statistic = 26.88, $n$ = 305, $P < 0.001$). In males, this age effect tended to advance to age 4, and was delayed thereafter (Figure 2B; difference between age 4 and 5: medians 15 and 17 April, KW-statistic = 3.85, $n$ = 91, $P$ = 0.049). All three extremely late arrivals (>15 May) were first-year males, and these individuals did not obtain a female. We may have missed several of these late arrivals, because at that time our focus was on breeding birds, rather than on new arrivals.

We found a similar age effect within individuals: in females arrival date in the first year of life was 3.37 days later than for the same individual returning in the second year (Figure 2; paired $t$-test of relative arrival dates: difference: 3.37 (1.32), $t$ = 2.36, $n$ = 36, $P$ = 0.015). For males we found no such difference (paired $t$-test: difference: 1.11 (2.12), $t$ = 0.53, $n$ = 26, $P$ = 0.60), although this is largely driven by birds born in 2012: in 2013, the six young males arrived within a narrow window, but were late in 2014 (see Figure 3). Without the 2012-cohort, young males arrived 3.86 (1.98) days later in their first than in their second year of life.

Many (especially male) individuals were not recorded in the study plots in their first year of life (but turned up in later years). Therefore we also analysed whether individuals first seen in their second year arrived later than in the third year. Males not seen in their first year of life tended to arrive 1.50 (0.81) days later in their second than in their third year ($t$ = 1.84, $n$ = 44, $P$ = 0.07). There was no difference in arrival date between second and third year in females (difference: –0.85 (1.31), $t$ = –0.65, $n$ = 29, $P$ = 0.52). Too few individuals were observed in all three years after birth to investigate whether this tendency is an age-effect, or due to inexperience in the recruitment year. However, the comparison between males breeding in their second year that had or had not bred in their first year did not suggest that inexperienced males arrived later (Figure 2; KW-statistic = 0.81, $n$ = 70, $P$ = 0.36).

**Arrival and laying date repeatability**

Spring arrival dates were repeatable in males and females for which we had repeated observations in multiple years. Repeatabilities on absolute arrival dates were lower for males (0.175, 95%-CI = 0.087–0.257) than for females (0.279, 95%-CI = 0.173–0.378; Table 3), but the difference was not significant (bootstrapped $P$-value on difference, $P$ = 0.15). Arrival dates relative to the annual mean were slightly more repeatable, and were similar for males (0.268, CI = 0.166–0.354) and females (0.300, CI = 0.191–0.391).

Laying date repeatability came close to arrival date repeatability in females, but was clearly lower in males (Table 2). In males the repeatabilities in relative arrival and laying dates differed significantly (mean laying date; 0.103, 95%-CI = 0.006–0.205, Bootstrap with arrival: $P$ = 0.018), and for absolute values there was also a tendency for a difference (mean laying date; 0.058, 95%-CI = 0–0.154, Bootstrap with arrival: $P$ = 0.07).

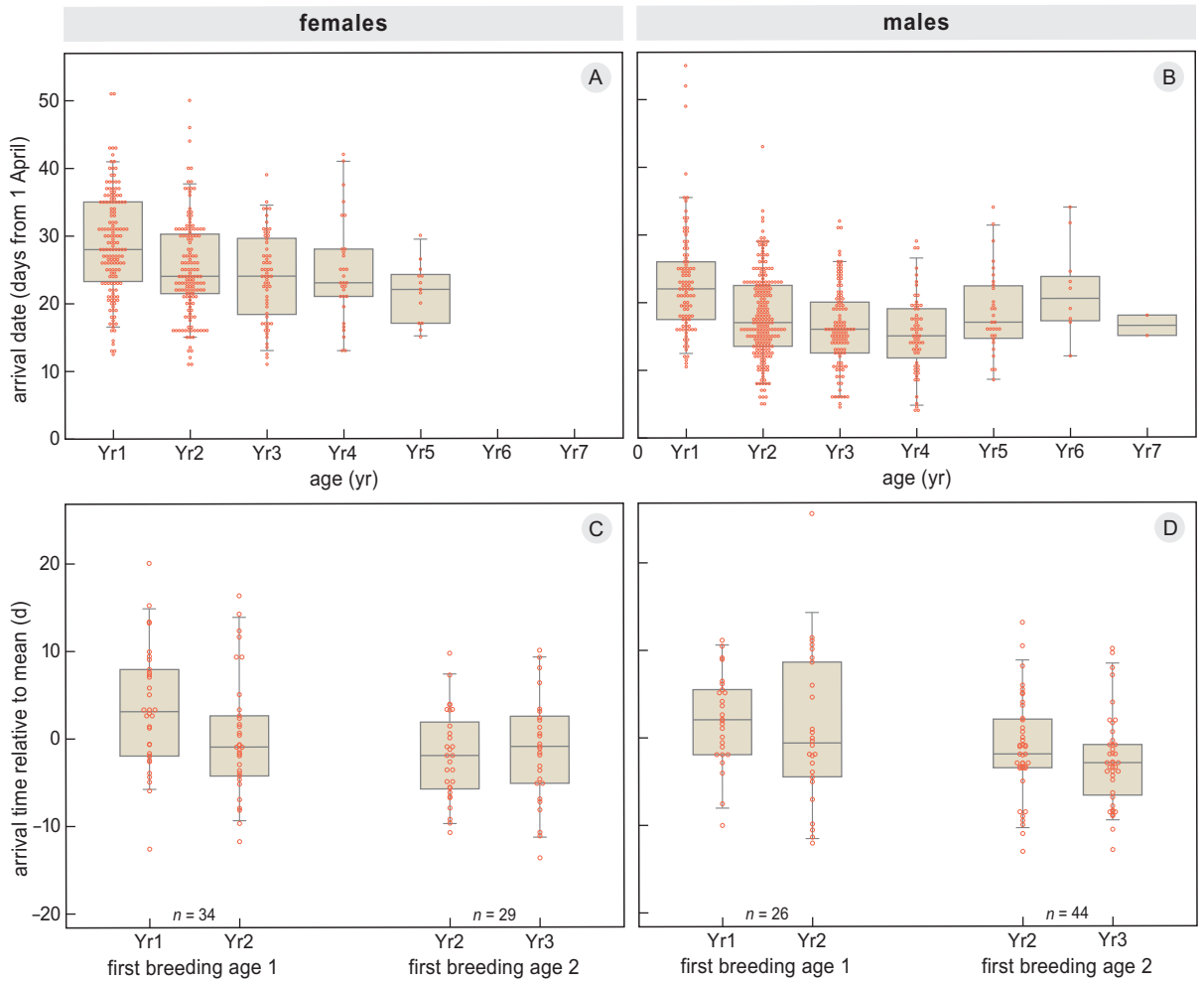


**Figure 2.** Spring arrival date in relation to age in Pied Flycatchers ringed as nestlings. (A) Absolute arrival date for all females with known age, (B) absolute arrival date for all males with known age, (C) relative arrival date to the annual mean for known age females breeding in two consecutive years, with the two left bars for females that were first observed breeding in their first year, and the two right bars for females first observed breeding in their second year, (D) idem for males. The box shows the 25–75%-percentiles, with the horizontal line being the median. Whiskers are the 5–95%-percentiles. Dots show the individual observations.

Repeatabilities in arrival dates between two consecutive years differed considerably (Figure 3, Table 3). In females between-year repeatability ranged from 0.23 for 2012–13 to 0.66 for 2010–11. Pair-wise comparisons for females showed only significant differences between 2010–11 and 2012–13, and between 2010–11 and 2013–14 (Bootstrapped *P*-values < 0.05). As with the overall repeatability, in males between-year repeatability was lower than in females (paired *t*-test on annual estimates, $t = 2.67$, $df = 5$, $P = 0.043$) and again showed substantial variation: the lowest repeatability was 0.17 for 2013–14, and the highest was 0.39 for 2011–12. Pair-wise comparisons for repeatability for males in groups of consecutive years did not show significant differences.

Consistency is the mean individual absolute difference between two consecutive years, and for female laying date this was 4.11 days across years (based on values relative to annual mean), with highest consistency between 2010–11 (only 2.81 d; note that a low value refers to a high consistency), and lowest between 2013–14 (5.99 d, overall significant difference among groups of years: $F_{5,244} = 7.47$, $P < 0.001$). For female arrival date the average was 5.27 d, ranging from 3.77 d in 2010–11 to 6.24 in 2013–14 (overall significant difference among groups of years: $F_{5,253} = 2.50$, $P = 0.031$; Table 3). For female arrival date and laying date, we found that consecutive years with higher consistency also had higher repeatability (arrival date: $r = -0.95$, $n = 6$, $P = 0.004$; laying date: $r = -0.86$, $n = 6$,

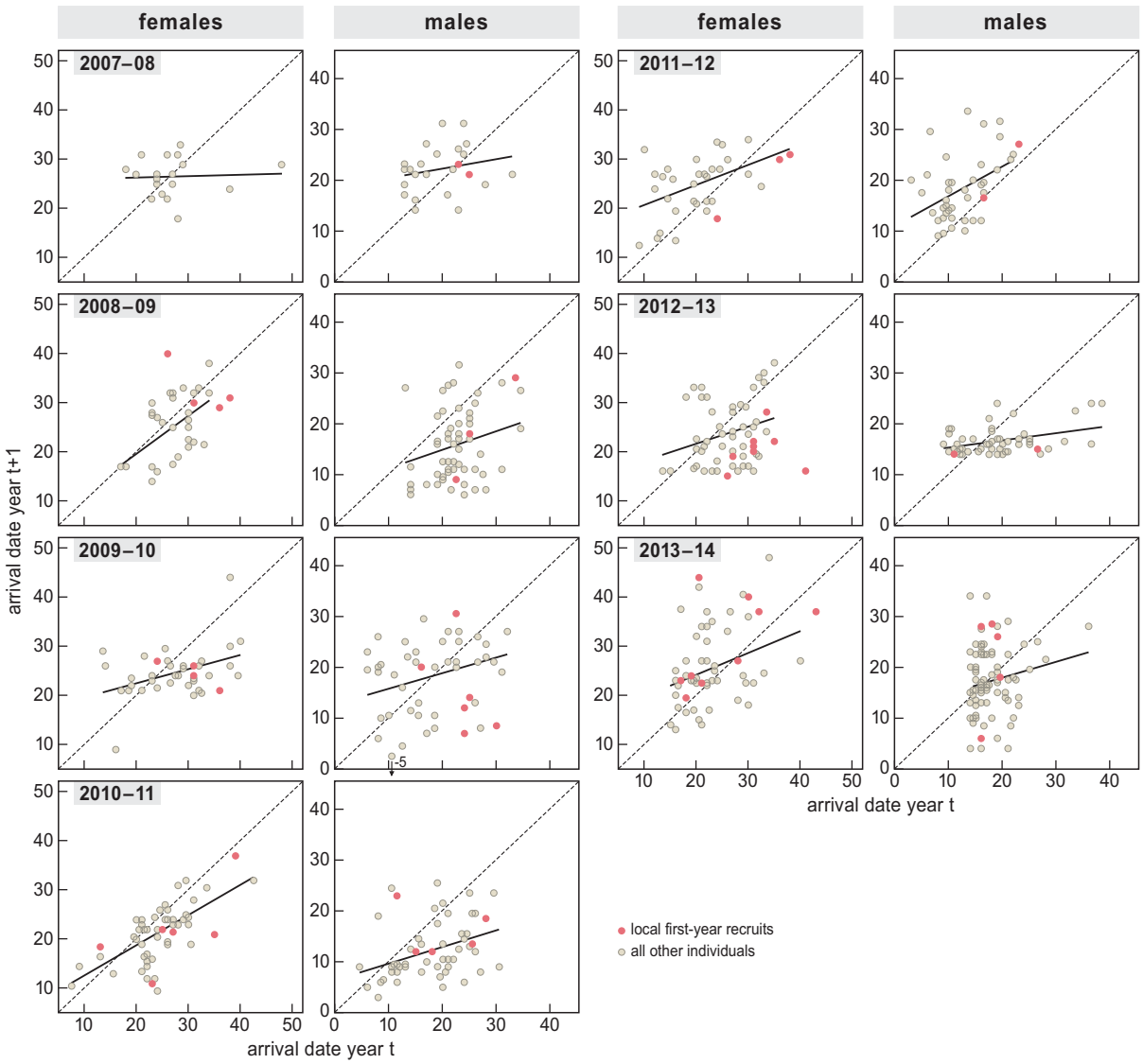


**Figure 3.** Arrival dates of individual Pied Flycatchers in two consecutive years in Drenthe, The Netherlands. Regression lines are based on values of individuals excluding the known first year birds. Left panels: females, right panels: males.

$P = 0.028$). In contrast, consistency in male arrival was lower (5.72 d), and varied less over time than in females, from 5.08 in 2011–12 to 7.28 in 2009–10 (no significant difference among groups of years: ANOVA on groups of years, $F_{5,316} = 1.78$, $P = 0.12$, for estimates see Table 3). Interestingly, for male arrival we found no correlation between consistency and repeatability ($r = -0.08$, $n = 6$, $P = 0.89$) suggesting that between-year variation in repeatability is not caused by changes in how consistent males are.

In females and males, between-year arrival date repeatability was positively correlated with between-year laying date repeatability, thus showing that if between-year repeatability in arrival date was higher, it was also higher for laying dates (Pearson's correlation: females: $r = 0.86$, $n = 6$, $P = 0.028$; males: $r = 0.75$, $n = 6$, $P = 0.09$). We found no consistent pattern that pairs of years that were high in repeatability for males were also high for females (Pearson's correlation on annual estimates: $r = 0.63$, $n = 6$, $P = 0.18$). In females we found no difference in between-year repeatability between arrival dates and laying dates (mean for arrival date: 0.41, mean for laying date 0.39; paired *t*-test: $t = 0.29$, $df = 5$, $P = 0.79$), whereas in males this was different (mean for arrival date: 0.28, mean for laying date 0.12; paired *t*-test: $t = 4.36$, $df = 5$, $P = 0.073$).

**Table 3.** Arrival date (A) and laying date (B) repeatabilities for individual female and male Pied Flycatchers for 2008–2014. For all observations of individuals with multiple observations we give repeatabilities for the absolute values, and the values relative to the annual mean for that sex. We also give the repeatability relative to the annual means for pairs of consecutive years, to show the temporal variation in repeatability. Cons is the consistency, expressed as the mean of absolute difference of relative dates in consecutive years. n is the number of individuals included.

| | Females | | | | | Males | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | Cons | Repeat | SE | *P* | *n* | Cons | Repeat | SE | *P* |
| **(A)** | | | | | | | | | | |
| Abs. arrival | 221 | | 0.279 | 0.053 | <0.001 | 307 | | 0.175 | 0.045 | <0.001 |
| Relative arrival | 221 | | 0.300 | 0.035 | <0.001 | 307 | | 0.268 | 0.028 | <0.001 |
| 2008–09 | 30 | 4.96 | 0.439 | 0.152 | 0.002 | 53 | 6.17 | 0.177 | 0.108 | 0.059 |
| 2009–10 | 36 | 5.67 | 0.401 | 0.138 | 0.003 | 43 | 7.28 | 0.321 | 0.169 | 0.007 |
| 2010–11 | 52 | 3.77 | 0.659 | 0.059 | <0.001 | 48 | 5.27 | 0.387 | 0.120 | 0.002 |
| 2011–12 | 33 | 5.13 | 0.446 | 0.150 | 0.002 | 41 | 5.08 | 0.386 | 0.127 | 0.003 |
| 2012–13 | 49 | 5.90 | 0.231 | 0.148 | 0.031 | 55 | 5.28 | 0.253 | 0.122 | 0.021 |
| 2013–14 | 55 | 6.24 | 0.281 | 0.147 | 0.018 | 82 | 5.23 | 0.168 | 0.087 | 0.061 |
| Total | 255 | 5.27 | 0.410 | | | 322 | 5.72 | 0.282 | | |
| **(B)** | | | | | | | | | | |
| Abs. Laying | 217 | | 0.216 | 0.031 | <0.001 | 257 | | 0.058 | 0.043 | 0.330 |
| Relative Laying | 217 | | 0.306 | 0.061 | <0.001 | 257 | | 0.103 | 0.034 | 0.043 |
| 2008–09 | 30 | 3.83 | 0.599 | 0.136 | <0.001 | 48 | 6.41 | 0.000 | 0.082 | 0.197 |
| 2009–10 | 35 | 4.77 | 0.346 | 0.1 | 0.011 | 36 | 6.50 | 0.072 | 0.109 | 0.141 |
| 2010–11 | 51 | 3.96 | 0.684 | 0.068 | <0.001 | 40 | 4.58 | 0.335 | 0.165 | 0.012 |
| 2011–12 | 32 | 4.38 | 0.505 | 0.135 | <0.001 | 38 | 6.00 | 0.156 | 0.096 | 0.124 |
| 2012–13 | 48 | 4.69 | 0.219 | 0.118 | 0.063 | 45 | 4.29 | 0.206 | 0.118 | 0.089 |
| 2013–14 | 54 | 7.50 | 0.000 | 0.066 | 0.322 | 45 | 6.82 | 0.000 | 0.103 | 0.232 |
| Total | 250 | 4.86 | 0.392 | | | 252 | 5.77 | 0.128 | | |

Repeatabilities of arrival for all observations of females were considerably lower than when measured on females in consecutive years (for relative arrival dates: 0.30 vs. 0.41; Table 3). A possible reason is that observations that come from consecutive years are more repeatable than observations that have more years in between. In females we indeed found support for such a difference: females from their first recorded year to the next year had a repeatability of 0.36 (SE = 0.064, 95%-CI = 0.283–0.467, $n$ = 156 females, relative arrival date), whereas the repeatability from the first to the third year was 0.23 (SE = 0.13, 95%-CI = 0.016–0.388, $n$ = 75 individuals). The reason is not that arrival becomes less repeatable throughout the life of an individual, because for females relative arrival date of the second to the third year of observation was even higher than from the first to the second ($R$ = 0.54, SE = 0.074, 95%-CI = 0.469–0.687, $n$ = 54). Also, if we exclude the first arrival date, repeatability does not increase (relative arrival date: $R$ = 0.34, SE = 0.059, 95%-CI = 0.228–0.411, $n$ = 73), suggesting that first-year arrivals are not less consistent than later-year arrivals.

## DISCUSSION

After a journey of 5000 km, Pied Flycatchers arrived at their Dutch breeding grounds over a period of several weeks. Individuals varied in their arrival dates, resulting in repeatability of this trait. This repeatability in arrival dates was similar between males and females, but only in females reflected in repeatability of laying dates, as males do normally not contribute to the timing of laying date of their partner (van Noordwijk *et al.* 1981), and the correlation between male arrival and pairing date varied between years and was on average not high. These results suggest that individuals have an innate spring timing schedule. However, our finding that in some combinations of consecutive years arrival

repeatability was notably lower, implies that environmental circumstances could disrupt the expression of this individual schedule at the end point of the migratory journey. Our observation that repeatability in female arrival is higher between consecutive years than when there is a year in between, suggests that carry-over effects may also influence arrival (Norris *et al.* 2004). Whereas the observed repeatability of c. 30% leaves ample opportunity for adaptive plasticity of arrival date in response to environmental conditions, our discussion is mostly focused on why individuals have rather consistent patterns, and why these vary in expression between years.

**Repeatability of arrival**

Consistent individual differences in arrival dates may arise from four processes before and during migration: individual variation in migration distance, departure time, duration of stop-overs and/or flight speed. Pied Flycatchers are known to be faithful to their wintering sites (Salewski *et al.* 2002), but this likely does not result in large within-population variation in migration distance. Recent geolocator data showed that our population is confined to a rather small wintering area (Ouwehand *et al.* 2015). More generally, Pied Flycatchers winter in a rather narrow latitudinal band covering the Sudanian woodlands in West-Africa (Dowsett 2010), which results in small variation in potential migration distance, if we assume that all birds take roughly the same routes. In contrast, Barn Swallows *Hirundo rustica* winter over a much wider area, and their spring arrival does correlate with latitude and longitude of the wintering sites, with birds at more northern and eastern wintering sites arriving earlier (Liechti *et al.* 2015).

Consistent variation in migration speed as the cause for the repeatability in arrival date is supported by data showing that longer-winged individuals arrive consistently earlier in Pied Flycatchers (Potti 1998) and Barn Swallows (Teplitsky *et al.* 2011). Assuming that longer-winged individuals fly faster than shorter-winged individuals, this could explain consistent variation in arrival time even if birds all depart at the same date. However, spring migration speed is already fast in Pied Flycatchers: Dutch, British and Finnish males with geolocators covered the distance between wintering and breeding grounds in c. 17 days, with little variation among individuals (Ouwehand *et al.* 2015). Based on the low variation in migration duration, we consider it unlikely that the observed variation in arrival date that spans often more than two weeks between the first and last 10% of the distribution (Table 2) is entirely caused by variation in migration speed.

For small passerines we consider consistent individual variation in departure dates as the most likely cause of the observed repeatability in arrival dates. Few studies have shown that arrival and departure dates were positively correlated, as in Great Reed Warblers *Acrocephalus arundinaceus* (Lemke *et al.* 2013) and Wood Thrushes *Hylocichla mustelina* (Stanley *et al.* 2012). Data from four Common Redstarts *Phoenicurus phoenicurus* indicated that arrival and departure were correlated, and two individuals tracked in consecutive years arrived later when departing later (Kristensen *et al.* 2013). Also, in lab studies individuals of the same populations have individually varying timing schedules (Pulido 2007). New data from our Pied Flycatcher population indeed shows that for 2014 there was a strong positive correlation between departure and arrival date (Ouwehand *et al.* in prep.), supporting our hypothesis that repeatability in arrival dates mostly comes from consistent individual differences in departure date from the wintering grounds.

The question remains: if individuals have a consistent departure date from the wintering grounds, why is repeatability in spring arrival so variable? Repeatability is the fraction of total phenotypic variance that could be attributed to the individual, and thus can be affected by how consistent individuals are and the amount of phenotypic variance present (see e.g. Conklin *et al.* 2013). For females, repeatability between combinations of consecutive years was largely explained by how consistent arrival was in individuals, suggesting that under some circumstances individuals could not express their normal individual schedule, resulting in low repeatability. The expression of these individual schedules is likely to be modified by environmental circumstances. In years with poor winter conditions, all birds may be delayed until spring rains arrive, and therefore the individual variation may disappear (Tøttrup *et al.* 2012, Kristensen *et al.* 2013). Initial differences in departure date can be equalized when birds hit unfavourable conditions during migration, with all birds queuing behind an adverse weather system, and then arriving synchronously upon improvement of weather conditions. The arrival peak in 2013 was, especially for males, likely to be caused by such an event, as cold conditions prevailed over Western Europe at the beginning of April and many males arrived synchronously after the wind turned to the south and temperatures increased (see supplementary Figure). Conditions during migration can also exacerbate initial departure variation, when early departing individuals happen to migrate under more favourable conditions than later ones. We thus predict that the

correlation between departure date from the wintering grounds and arrival date on the breeding grounds differs strongly between years, but we lack data on departure dates for multiple years to test this.

Repeatability of arrival date showed large variations between years, but we found significant differences among groups of years only in females. Even with our large sample sizes, the estimates have rather large confidence intervals and therefore little power. Still, variation in repeatability between years is larger in females than males (Table 3), and females show between-year variation in consistency, whereas in males we could not detect such a difference. This could be interpreted as female timing schedules being more affected by environmental circumstances than those of males. Alternatively, protandry may expose males to more adverse weather conditions during migration and upon arrival, resulting in selective mortality among early birds (Brown & Brown 2000), whereas in warm years the later males will not obtain a nest box and for that reason are not observed (e.g. Sternberg *et al.* 2002). Selective disappearance may thus reduce the phenotypic variance, and especially affect the individuals at the extremes, thereby reducing the observed repeatability for surviving individuals. These results hint at important differences between sexes in their responses to environmental circumstances, suggesting that flexible phenotypic responses may be more prominent in females, whereas the observed phenotypic variance in males more likely results from selective disappearance.

**Comparison with other studies**

Spring arrival date has been shown to be repeatable in many studies, across a wide array of species (Table 1), and only a few studies did not find significant repeatability (Potti 1998, Cooper 2008, Muller *et al.* 2014). Studies however varied in their estimates, from a low but significant value of 0.09 in a very large sample of Cliff Swallows *Petrochelidon pyrrhonota* (Brown & Brown 1998), to a high value of 0.67 in a small sample of Black Kites *Milvus migrans* tagged with a satellite-transmitter (Sergio *et al.* 2014). Various recent studies have used small samples of mostly large-bodied tagged birds. These studies were accurate in determining arrival date and often found high repeatability. Studies that rely on field observations of individually recognizable individuals need larger sample sizes.

The variance between studies in the estimate of arrival date repeatability could be due to real differences among species/populations, but also the result of year-dependent estimates or the result of different methodologies. Starting with the latter, some studies have analysed males and females simultaneously (e.g. Gill *et al.* 2014, Sergio *et al.* 2014), and if sexes arrive on average at different times (as is often the case: current study, Lourenço *et al.* 2011, Gordo *et al.* 2013, Coppack *et al.* 2006), the repeatability may be an effect of sex, rather than of individual variation within sexes. Some studies have standardized arrival dates to the annual mean, whereas other have not. When a trend is observed in arrival date over the years or temporal autocorrelation occurs, a lack of standardizing will increase repeatability, as most individuals are only measured in a restricted period of years (e.g. Møller 2001). Arguably, standardization has the disadvantage of reducing phenotypic variation, and thereby increasing repeatability for the same level of consistency. A final methodological issue is whether birds were sampled from a wintering or breeding population, or both. For example, Conklin *et al.* (2013) sampled a Bar-tailed Godwit *Limosa lapponica* population wintering in New Zealand, and based on geolocator data found an extremely high repeatability of breeding ground arrival. However, birds migrated to different latitudes in Alaska, and including this latitudinal effect reduced the individual component to a large degree. The high arrival repeatability of Wood Thrushes could also be a consequence of between-breeding population and between-sex variation (Stanley *et al.* 2012).

Although few studies have considered sex-specific arrival repeatability within populations, the few studies doing so found higher repeatability estimates among females than among males (Black-tailed Godwits *Limosa limosa*, Eastern Kingbirds *Tyrannus tyrannus*, Pied Flycatchers; Table 1). Our data are to some degree consistent with this pattern, as for non-standardised arrivals males had a lower repeatability estimate than females, as was the case when considering groups of consecutive years (Table 3). With so few studies it is unclear whether this is a common pattern, but as hypothesized before, males arrive earlier and under harsher conditions than females, and hence selective disappearance (and thus reduced observed between-individual variation) may be more common in males.

Departure dates from the wintering grounds and stop-over sites are less often studied, but these show similar repeatabilities as well (Table 3). Most studies however do not separate males and females, whereas lab data on song birds show that sexes often depart at different times (Coppack & Pulido 2009), and sexes may differ in their repeatability.

**Age effect**

First-year birds arrived later than older birds, as has been found in several other species of long-distance migrants (Hill 1989), including Pied Flycatchers. In Spain the difference between first- and second-year males was about five days, and arrival date advanced up to the 3rd year (Potti 1998), similar to our study. The reason for the later arrival of young birds is unclear. In an earlier study based on ring recoveries in North Africa (Both 2010), first-year Pied Flycatchers from the same latitudes as our population were recovered about 10 days later than older birds (SE = 2.16, $n$ = 160, reanalysis of a subset of this dataset: only birds from 1975–2003, and born south of 57°N included; year of recovery included in this model). This suggests that they may depart later or get delayed during the crossing of the Sahara. Furthermore, the difference between age classes in these recoveries is more than twice the difference observed in arrival date of about five days. Although later departing individuals may travel faster, recent tracking data showed that first-year Wood Thrushes departed later, but also travelled slower, and thereby increased the delay relative to older individuals (McKinnon *et al.* 2014). We consider it likely that also in Pied Flycatchers young may migrate slower and depart later, and that late arriving individuals are not observed because they do not start singing or breeding. As mentioned earlier, a large fraction of the population is not observed breeding locally in their first year, and these may indeed be the birds arriving too late. Hence, our estimate of first-year arrival may be biased towards the successful individuals. The reason why young birds may travel slower and arrive later could be inexperience (Sergio *et al.* 2014), but also that their probability to breed is low, and therefore they take less risks during migration (Hill 1989).

In the available data in the literature, young birds show consistently lower repeatability in arrival date compared to older birds (Table 1: Black Kites, Bar-tailed Godwits, Common Terns *Sterna hirundo*, Eastern Kingbirds). This also suggests that young birds still need to learn how to migrate, and therefore show larger variability in arrival dates (Sergio *et al.* 2014).

**Implications of temporal variability**

The observed between-year variation in repeatability implies that in some years individually determined time schedules are expressed, whereas in other years these are blurred by environmental effects. It is still mere speculation whether these individual schedules are the result of genes (Pulido 2007, Tarka *et al.* 2015), ontogeny (Both 2010, Gill *et al.* 2014, Sergio *et al.* 2014) and/or winter habitat quality (Studds & Marra 2011, Kristensen *et al.* 2013), although all may contribute to different degrees in different populations (Charmantier & Gienapp 2014). If these individual schedules indeed exist, directional environmental change may either reinforce their expression or depress it. With climate change, the environmental conditions during spring migration may improve, and hence the expression of individual time schedules. If these individual schedules have a genetic basis, this could lead to a positive feedback in the evolutionary process, because heritabilities rise, assortative mating for arrival date likely increases, and selection thereby gets stronger. The lack of heritability at present (e.g. Potti 1998) may thus not be an absolute constraint in the future, as the expression depends on environmental effects. The same line of reasoning can also go in the opposite direction. Environmental deterioration at the wintering grounds or during migration may constrain the expression of individual annual schedules, and therefore heritabilities drop, and selection increasingly operates on the environmental variance of the phenotype. If sexes differ in how they are affected by environmental conditions, this may complicate matters further. Predicting the consequences and constraints of life-cycle adaptation of long-distance migrants to environmental change thus requires a better understanding of the ecological conditions these birds encounter during their winter and spring migration. The current development of tracking devices helps enormously to identify the sites important in their life-cycle, but only long-term field work in situ would suffice to include the relevant spatio-temporal variation in ecological conditions that affects these birds along their flyway.

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## SAMENVATTING

Voor trekvogels is het van belang om op het goede moment in het voorjaar in het broedgebied te arriveren. Als vogels te vroeg aankomen, is er nog weinig voedsel en kunnen ze doodgaan van de honger. Maar als ze te laat aankomen, is de voorjaarspiek in het voedsel achter de rug en lijden hun jongen honger. Evolutie zou moeten hebben geselecteerd op vogels die op het optimale moment arriveren. Binnen populaties is een aanzienlijke variatie in aankomstdatum waargenomen. Individuen blijken echter vaak consistent vroeg of juist laat te arriveren. Dit patroon vinden evolutionair biologen interessant, omdat het suggereert dat verschillen tussen individuen een genetische basis hebben. Een overzicht van studies naar de overeenkomst in aankomstdatum in het broedgebied bij trekvogels tussen jaren laat zien dat er grote verschillen bestaan tussen soorten en studies. Onze hypothese is dat deze variatie voor een deel kan worden verklaard door condities die trekvogels tijdens hun trek tegenkomen. In het hier besproken onderzoek geven we een overzicht van acht jaar waarnemingen van aankomstdata van Bonte Vliegenvangers *Ficedula hypoleuca* in ZW-Drenthe. Door dagelijks alle nestkasten af te lopen bepaalden we wanneer een individuele vogel was aangekomen in het broedgebied. Deze metingen bleken heel nauwkeurig te zijn, want de veldwaarnemingen kwamen bijna exact overeen met de aankomsten die werden berekend op basis van uitlezing van dataloggers van 13 individuen. Van meer dan 500 individuen hebben we de aankomstdatum voor meer dan één jaar tot onze beschikking. Tussen jaren vonden we duidelijke verschillen in gemiddelde aankomstdatum. Binnen jaren was de variatie in aankomstdatum binnen een sekse altijd meer dan twee weken. Eén jaar oude vliegenvangers kwamen 4–5 dagen later aan dan oudere vogels. Mannetjes kwamen gedurende hun eerste vier levensjaren steeds vroeger aan. Voor individuele vogels van beide seksen vonden we dat het verschil in aankomstdatum tussen jaren veel kleiner was dan het verschil tussen individuen binnen een jaar. Bovendien was de aankomstdatum voor individuele vogels vrij constant. Ook vonden we dat voor sommige paren de verschillen tussen opeenvolgende jaren veel groter waren dan voor andere paren. Bij vrouwtjes was de overeenkomst in aankomstdatum tussen jaren vergelijkbaar met de overeenkomst in legdatum tussen jaren, maar bij mannen was dat veel minder het geval. We denken dat het verschil in overeenkomst van de aankomstdatum tussen opeenvolgende jaren komt doordat vogels een individueel bepaalde vertrekdatum hebben uit Afrika, maar dat de vogels in sommige jaren voor of tijdens de trek zijn opgehouden. Zo kunnen droge jaren in tropisch Afrika maken dat vogels pas later kunnen vertrekken. Of slechte omstandigheden onderweg kunnen ertoe leiden dat vogels worden opgehouden en dan massaal en gelijktijdig arriveren zodra het weer verbetert (bijvoorbeeld in 2013). Deze variatie is interessant voor evolutiebiologen, omdat in sommige jaren de mogelijk aanwezige genetische variatie in trektijden misschien niet tot uiting komt, en in andere jaren juist wel. In een snel veranderende wereld kan flexibiliteit in aankomstdatum van groot belang zijn. Het is belangrijk om te begrijpen hoe dat in zijn werk gaat, en of micro-evolutie kan plaatsvinden op de aanwezige variatie.

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## SUPPLEMENTARY MATERIAL

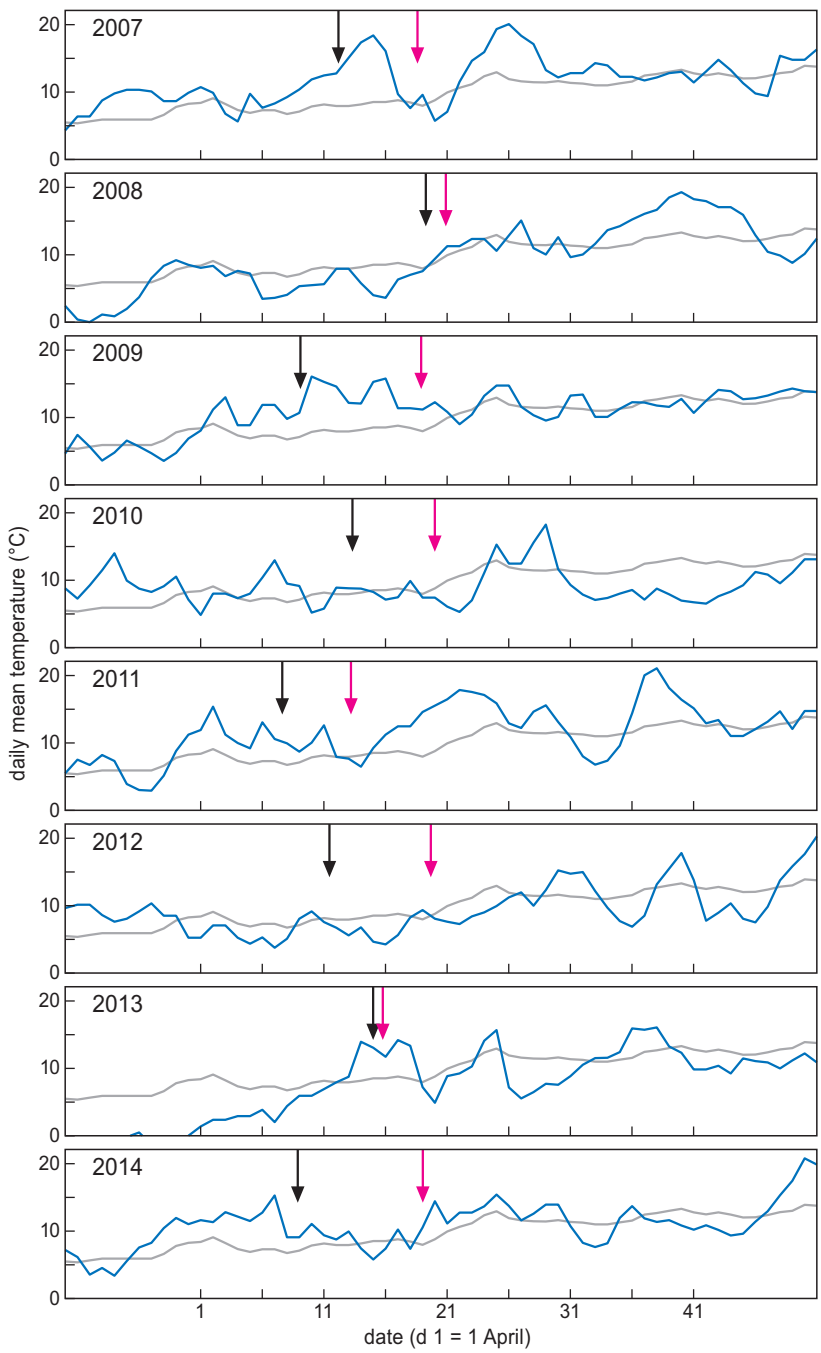


**Figure S1.** Daily mean temperatures in the study area from 20 March – 10 May. For comparison the daily mean for the period 1990–2014 is also given (grey line). Black arrows denote the date when 10% of the males had arrived, pink arrows idem for females.